

# Food Habits of Several Abundant Zooplankton Species in the Sacramento-San Joaquin Estuary

James J. Orsi  
California Department of Fish and Game

Technical Report 41

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Interagency Ecological Program  
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## ABSTRACT

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Gut contents of several zooplankton species were examined with phase-contrast and scanning electron microscopy. The copepods *Eurytemora affinis* and *Sinocalanus doerrii* consumed mostly diatoms, of which *Thalassiosira* spp. and *Skeletonema potamos* were the most abundant. The cladocerans *Daphnia parvula* and *Bosmina longirostris* ate mainly green and blue-green algae. The chain-forming diatom *Melosira granulata* was eaten by all zooplankton, but copepods appeared to consume it only when it was not blooming. Other than flagellated protozoans, animal remains were not found in zooplankton gut contents.

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## ACKNOWLEDGMENTS

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I thank Jack Pangborn, retired director of the Facility for Advanced Instrumentation, for SEM training. George Weber, retired Department of Water Resources biologist, guided me in the phytoplankton identifications. Don Stevens and Charles Armor, Department of Fish and Game; Wim Kimmerer, Biosystems Analysis Inc.; and Peggy Lehman, Department of Water Resources, reviewed the manuscript. Funding for the work was provided by the Environmental Protection Agency under grant C060000-21. James Sutton, State Water Resources Control Board, obtained the grant and reviewed an earlier version of the manuscript, as did Daniel Otis, also of the Board.

## INTRODUCTION

Monitoring of zooplankton abundance in Suisun Bay and the Delta (Figure 1) by the Department of Fish and Game as part of the Interagency Ecological Program began in 1972 under authorization by State Water Resources Control Board Decision 1379. Data from the zooplankton monitoring study and Department of Water Resources phytoplankton monitoring show that zooplankton and phyto-

plankton concentrations started to decline in the early 1970s (Phytoplankton Task Force 1984; Orsi and Mecum 1986; Obrebski *et al* 1992). In addition to the decrease in phytoplankton, beginning in 1980 phytoplankton blooms shifted from *Skeletonema* and *Thalassiosira* to *Melosira granulata*, a diatom that forms long chains (Lehman and Smith 1991).

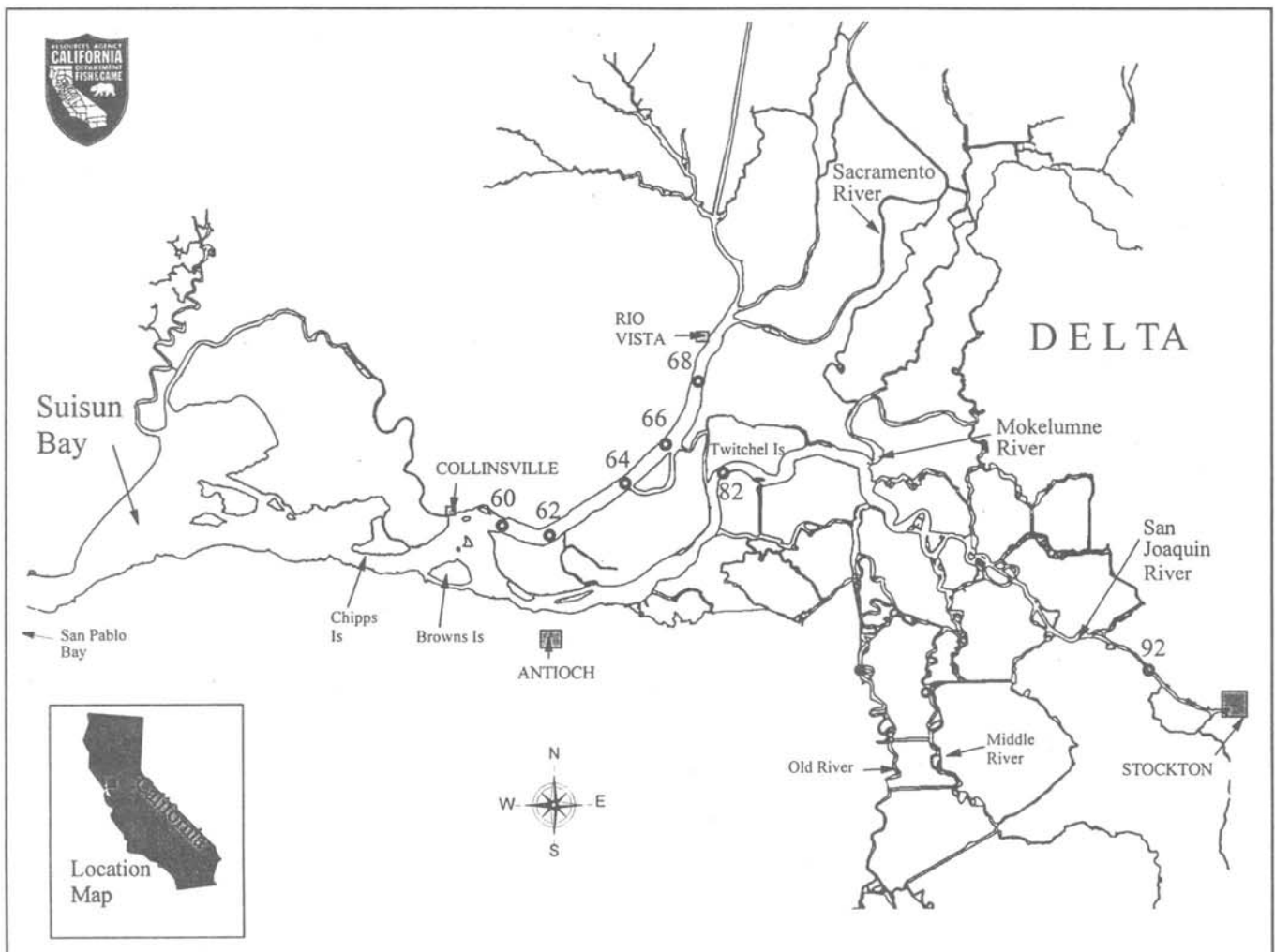


Figure 1  
Sampling Locations, Zooplankton Monitoring Study

A study of the food habits of the native copepod *Eurytemora affinis*, the accidentally introduced *Sinocalanus doerrii*, and the cladocerans *Daphnia* and *Bosmina* was funded in 1986 by the State Water Resources Control Board, and a report was prepared (Orsi 1988). That report is revised here for publication as an Interagency Ecological Program Technical Report.

Specific objectives of this report are to determine what phytoplankton was con-

sumed, whether the copepods were predatory, whether the long chains of *M. granulata* were consumed, and how similar were the food habits of the two copepods and two cladocerans. The copepods have somewhat different but extensively overlapping distributions. *E. affinis* is most abundant in the entrapment zone, and *S. doerrii* is most abundant somewhat upstream from there. The cladocerans are freshwater animals whose abundance peaks in the San Joaquin River near Stockton.



## METHODS

The gut contents of zooplankton were examined from the DFG zooplankton monitoring samples (Orsi and Mecum 1986) collected in May and June, during blooms (chlorophyll *a* >15 µg/L) of *M. granulata* and *Skeletonema potamos*, another chain-forming diatom. Gut contents were also examined from samples taken in the same months but when or where blooms did not occur. Dates, areas, conditions, and zooplankton examined are:

Period A, 5/16/86, Suisun Bay *S. potamos* bloom, *E. affinis* and *S. doerrii*;

Period B, 6/13/85, Suisun Bay non-bloom, *E. affinis* and *S. doerrii*;

Period C, 5/13/85, Delta *M. granulata* bloom, *Daphnia* and *Bosmina*;

Period D, 6/24/85, Delta non-bloom, all species.

Most copepods found during the *M. granulata* bloom had empty guts; hence, copepods were not included in Period C.

Zooplankton specimens were picked out of samples, and fecal pellets in their guts were dissected out of the animals with

fine needles, placed in a drop of glycerin, and the contents dispersed by adding a cover slip and applying gentle pressure. Using phase-contrast microscopy at 750x, algae and other organisms were identified, counted and measured. Cell volumes were calculated by matching the shapes of cells to the closest geometrical shape (eg, cones, ovals, spheres) or some combination of such shapes and applying the appropriate mathematical formulas.

A scanning electron microscope (Jeol S130 located at the Facility for Advanced Instrumentation, University of California, Davis) was used on samples taken on other dates for identification, photographs, and overall view of food consumed. Fecal pellets, either dissected from the zooplankton as above or voided by living zooplankton brought back to the laboratory, were kept in water for 24 hours or more so bacteria could decompose the peritrophic membrane surrounding them (Turner 1984). The pellets were then placed on aluminum stubs and either left intact or broken open, air-dried, gold-coated, and examined at an accelerating voltage of 10 KV.

## COMPOSITION OF GUT CONTENTS

The copepods consumed a variety of solitary and chain-forming centric and pennate diatoms, green and blue-green algae, flagellated protozoans and miscellaneous items such as fungi, pollen grains, and bacteria (Figures 2-6, Tables 1-3).

Diatoms constituted >90% of the volume of the gut contents of both copepods during Periods A, B, and D (Figure 7). The abundance of green and blue-green algae varied with period and species of copepod. They were most abundant during period B, the Suisun Bay non-bloom, for both species.

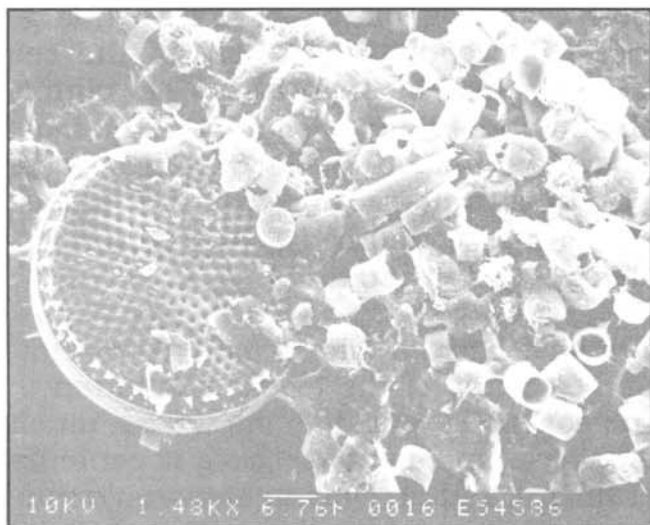


Figure 2

*Eurytemora affinis* gut contents showing *Thalassiosira lacustris* (large cell) and mass of *Skeletonema potamos* with a single cell of *Melosira granulata* var. *angustissima* (long cell just above center). Taken from the Sacramento River at Decker Island, 7/29/85. The legend below the micrograph indicates an accelerating voltage of 10 KV and a magnification of 1630 times. The line is a scale bar showing 6.14  $\mu$ m.

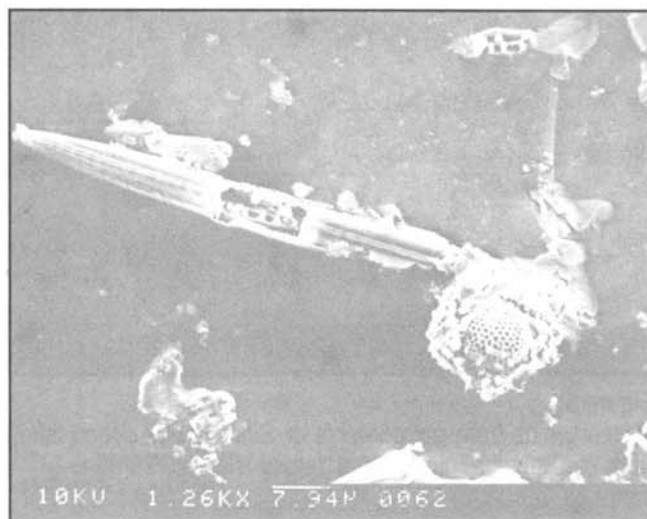


Figure 3

*Sinocalanus doerrii* gut contents showing *Nitzschia* (elongated cell) and *Thalassiosira* (lower right) taken from Suisun Bay at Chipps Island, 5/1/85.

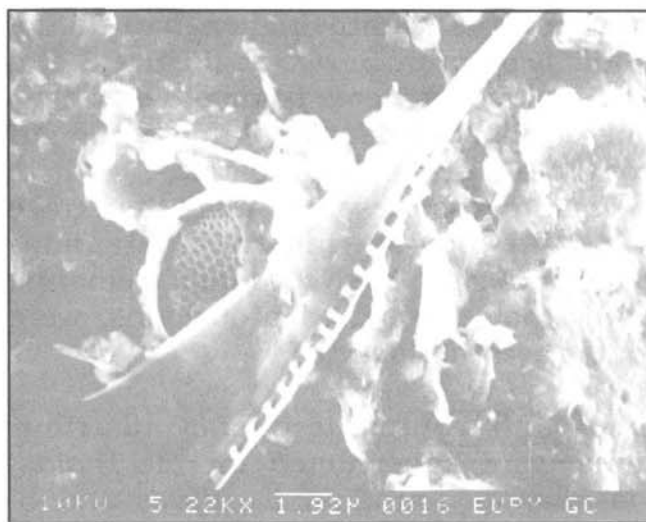


Figure 4

*Nitzschia* and *Thalassiosira* from gut contents of *Eurytemora affinis* taken in Sacramento River at Collinsville, 8/9/85.

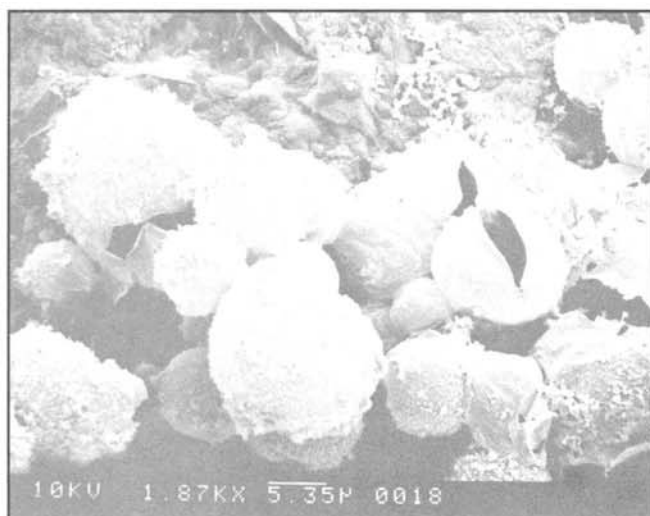


Figure 5  
Pollen grains from gut contents of *Sinocalanus doerrii* taken from the San Joaquin River at Jersey Island, 5/28/86.

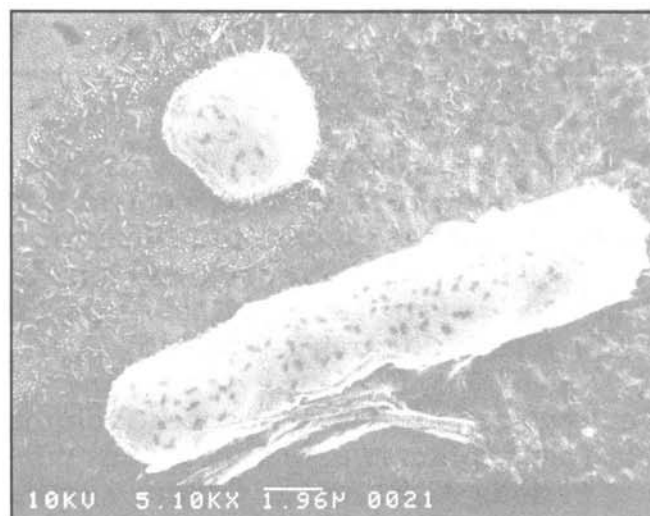


Figure 6  
Bacteria from gut contents of *Eurytemora affinis* taken from the San Joaquin River at Jersey Island, 5/28/86.

*Thalassiosira* spp. were volumetrically the most abundant diatoms in both copepods except during Period A, the *S. potamos* bloom, when the volume of *S. potamos* was slightly higher than that of *Thalassiosira* in *S. doerrii* (Figure 8 and Table 1). *Skeletonema potamos* comprised only a relatively small volume of the gut contents during other periods, and *M. granulata* was present in more than trace amounts only during the Delta non-bloom, Period D. No animal remains, other than flagellated protozoans, were found in either species.

Size- and volume-frequency distributions were constructed for all *Thalassiosira* spp. found in *E. affinis* and *S. doerrii* during all periods combined (Figures 9 and 10). Both copepods fed mainly on cells  $\leq 16 \mu\text{m}$  in diameter, but *S. doerrii* tended to consume more of the smallest cells ( $< 8 \mu\text{m}$ ) than *E. affinis* did. Cells  $\geq 16 \mu\text{m}$  in diameter were rare in

both copepods but, because of their large size, they constituted most of the cell volume consumed. In terms of volume, the 30 and 40  $\mu\text{m}$  classes were the most important ones to *S. doerrii*. These were also important size classes for *E. affinis*, which also consumed cells  $> 40 \mu\text{m}$ , although *S. doerrii* did not.

*Daphnia parvula* and *B. longirostris* consumed many of the food items found in the copepods, but diatoms were a much smaller component of the gut contents (Tables 4 and 5). Only in *D. parvula* during the *M. granulata* bloom (Period C) did diatoms comprise the largest component of the food volume (Figure 11). Strangely, the bloom was dominated by *M. varians*, not *M. granulata*. However, *M. granulata* made up most of the diatom volume in *B. longirostris* during the bloom and more than half the diatom volume in *D. parvula* during the non-bloom period.

Table 1  
Food Items in the Gut Contents of 32 *Eurytemora affinis* and 30 *Sinocalanus doerrii* during Period A,  
the Suisun Bay *Skeletonema potamos* Bloom

(All specimens were taken at Chipps Island at <0.5‰ S)

	<i>E. affinis</i>		<i>S. doerrii</i>	
	Cell Count	Volume ( $\mu\text{m}^3$ )	Cell Count	Volume ( $\mu\text{m}^3$ )
Diatoms				
Skeletonema potamos	7,185	538,875	6,921	604,997
Thalassiosira	273	772,084	157	581,206
Cyclotella	4	2,477	7	1,738
Cymatopleura			2	3,417
Melosira granulata	1	400		
Gomphonema	1	126		
Navicula	1	176		
Total	7,465	1,314,138	7,087	1,191,358
Green Algae				
Chlamydomonas	22	2,488	13	2,075
Flagellated algae	15	171	27	291
Trachelomonas	9	650	1	209
Scenedesmus quadricauda			8	226
Scenedesmus	4	226	1	56
Chodatella	1	268		
Tetrastrum staurogeniaeformae	4*	134		
Elakatotrix			2	56
Total	55	3,937	52	2,913
Blue-Green Algae				
Anacystis cyanea	231	5,186	98	6,414
Anacystis incerta			37	523
Coccochloris	13	106		
Total	244	5,292	135	6,937
Other				
Flagellated protozoa	26	1,249	20	200
Fungus spores	8		5	
Fungus	1			
Bacteria (chain)	4			
Total	39	1,249	25	200
Grand Total	7803	1,324,616	7299	1,201,408

\* Colonies

Table 2  
Food Items in the Gut Contents of 51 *Eurytemora affinis* Taken from Middle Point (5.3‰ S) and 30 *Sinocalanus doerrii* Taken from Chipps Island (2.6‰ S) and Browns Island (1.8‰ S) during Period B, the Suisun Bay Non-Bloom.

	<i>E. affinis</i>		<i>S. doerrii</i>	
	Cell Count	Volume ( $\mu\text{m}^3$ )	Cell Count	Volume ( $\mu\text{m}^3$ )
<b>Diatoms</b>				
Thalassiosira	314	551,547	166	185,785
Skeletonema potamos	108	10,800	118	7,788
Cyclotella	11	4,944	22	16,611
Nitzschia	1	180	2	520
Fragilaria			5**	240
Achnanthes			1	200
Cymbella	1*	945	*	
Melosira granulata	1*	200	1*	200
Cymatopleura	1	1,280		
Diatoma	1*			
Navicula	*			
Surirella			*	
Synedra	1	1,050	*	
Unidentified pennates			*	
Total	438	596,666	316	212,624
<b>Green Algae</b>				
Chlamydomonas	63	4,223	81	7,988
Flagellated algae	32	868	11	221
Scenedesmus	7	1,708	8	840
Trachelomonas	4	327	1	113
Total	106	7,125	316	9,162
<b>Blue-Green Algae</b>				
Anacystis incerta	308	7,265		
Anacystis cyanea	111	4,355	24*	1,899
Agmenellum	28	167		
Oscillatoria			5*	942
Coccochloris	6	85		
Total	453	11,872	29	2,841
<b>Other</b>				
Flagellated protozoa	23	892	53	2,792
Fungus spores	51		4	
Cosmarium			1	283
Total	74	892	58	3,075
Grand Total	1071	616,555	504	227,702

\* Plus fragments

\*\* Chain

Table 3  
Food Items in Gut Contents of 32 *Eurytemora affinis* Taken from the Sacramento River, Station 62 (2.3‰ S) and  
42 *Sinocalanus doerrii* Taken from Stations 62 to 66 (to 2.3‰ S) during Period D, the Delta Non-Bloom

	<i>E. affinis</i>		<i>S. doerrii</i>	
	Cell Count	Volume ( $\mu\text{m}^3$ )	Cell Count	Volume ( $\mu\text{m}^3$ )
Diatoms				
Thalassiosira	114	114,391	55	64,110
Skeletonema potamos			64	2,714
Cyclotella			5	9,632
Surirella	1	1,280	1	5,118
Melosira granulata	9*	4,021	4	4,001
Achnanthes			1	150
Unidentified pennates	2	200		
Total	126	119,892	130	28,026
Green Algae				
Chlamydomonas			5	37
Kirchneriella			4	267
Filamentous alga			4	
Scenedesmus			2	100
Flagellated algae			2	101
Ankistrodesmus			1	30
Total			23	535
Blue-Green Algae				
Anacystis cyanea	19	1,243	3	196
Agmenellum			6	3
Total	19	1,243	9	199
Other				
Flagellated protozoa			10	251
Fungus spores	1		2	
Fungal hyphae			1	
Total	1		13	251
Grand Total	146	121,135	175	86,710

\* Plus fragments

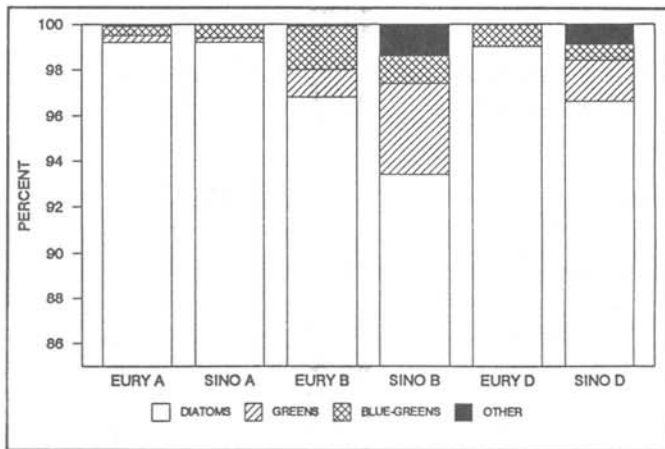


Figure 7  
Percent composition of gut contents of *E. affinis* and *S. doerrii* during Periods A, B, and D.

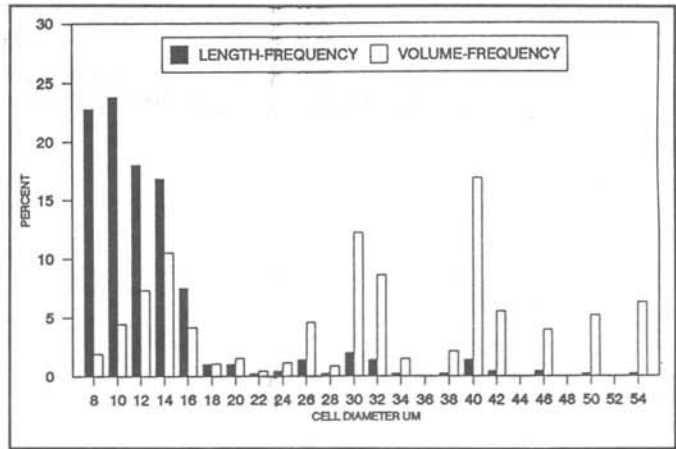


Figure 9  
Length-frequency and volume-frequency of *Thalassiosira* cells found in *E. affinis* during Periods A, B, and C combined.

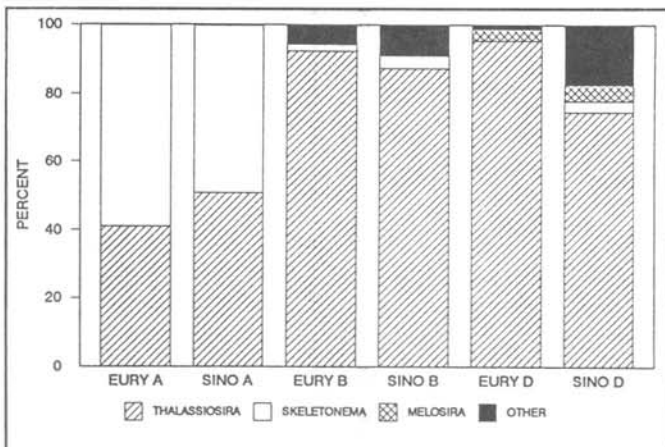


Figure 8  
Percent composition of diatoms in gut contents of *E. affinis* and *S. doerrii* during Periods A, B, and D.

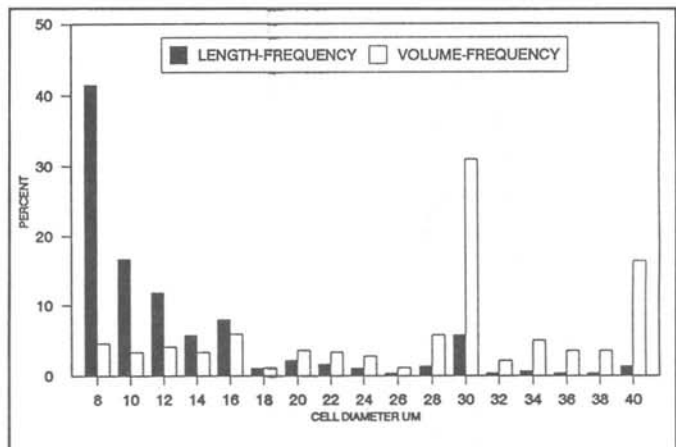


Figure 10  
Length-frequency and volume-frequency of *Thalassiosira* cells found in *S. doerrii* during Periods A, B, and D combined.

Table 4  
Food Items Found in 33 *Daphnia parvula* Taken from the San Joaquin River near Stockton (Station 92) and  
30 *Bosmina longirostris* Taken from the San Joaquin River near Twitchell Island (Station 82),  
Period C, Delta *Melosira granulata* Bloom

(All specimens from fresh water.)

	<i>D. parvula</i>		<i>B. longirostris</i>	
	Cell Count	Volume ( $\mu\text{m}^3$ )	Cell Count	Volume ( $\mu\text{m}^3$ )
Diatoms				
Thalassiosira	22	37,550	13	3,158
Melosira varians	10	53,078		
Melosira granulata	6*	8,520	21	26,389
Cyclotella	2**		1	130
Cymbella	2**			
Pennate species	11*		1**	
Total	53	99,148	36	29,677
Green Algae				
Chlamydomonas	412	74,160	435	78,127
Scenedesmus quadricauda (colony)	12	1,872		
Scenedesmus armatus (colony)	4	180		
Crucigenia (colony)	4	57		
Pteromonas	4	1,604	1	575
Chlorella	3	804		
Flagellated algae	3	180	3	31
Arachnochloris or Akanthochloris	2	524	2	523
Scenedesmus	1	288		
Trachelomonas	1	113		
Chodatella	1	8		
Chrysochromulina			4	360
Total	447	79,790	445	79,616
Blue-Green Algae				
Anacystis cyanea	46	3,011	7	458
Lyngbya	15*	19,301		
Cyanarcus hamiformis	2	603		
Agmenellum			90	377
Total	62	22,915	97	835
Other				
Flagellated protozoa	9	4,476	5	132
Fungus spores	4		1	
Total	13	4,476	6	132
Grand Total	575	206,329	584	110,260

\* Short chains

\*\* Fragments



Table 5  
Food Items Found in 25 *Daphnia parvula* Taken from the San Joaquin River near Stockton (Station 92) and  
25 *Bosmina longirostris* from the San Joaquin River at the Mouth of the Mokelumne River (Station 86),  
Period D, Delta Non-Bloom

(All specimens from freshwater.)

	<i>D. parvula</i>		<i>B. longirostris</i>	
	Cell Count	Volume ( $\mu\text{m}^3$ )	Cell Count	Volume ( $\mu\text{m}^3$ )
Diatoms				
Thalassiosira	4*	1,200	2	654
Melosira granulata	1*	1,256	1*	576
Pennate species	11*		*	
Cyclotella			1	300
Unidentified	4**			
Total	20	2,456	4	1,530
Green Algae				
Chlamydomonas	343	61,604	3	421
Flagellates	7	783	6	650
Scenedesmus sp. (colony)	2	96		
Scenedesmus quadricauda	1	288		
Total	353	62,771	9	1,071
Blue-Green Algae				
Anacystis sp.	484	31,679	1	20
Agmenellum (colonies)	134	1,894		
Total	538	33,573	1	20
Other				
Phacus	18	2,421	3	1,418
Flagellated protozoa	7	1,204	4	2,205
Glenodinium quadricens	3	170		
Glenodinium sp.			1	268
Fungus spores	2			
Glenodinium sp.	2	57		
Amphidinium	1	181		
Total	33	4,033	8	3,891
Grand Total	944	102,833	32	6512

\* Plus fragments

\*\* Fragments

Green and blue-green algae were large constituents of the gut contents of *D. parvula* in Periods C and D (Table 4, Figure 11). Flagellated protozoans were the largest constituent of the food volume in *B. longirostris* in Period D. Both cladocerans, especially *B. longirostris*, contained a large quantity of unidentifiable material, much of which appeared to be mineral particles.

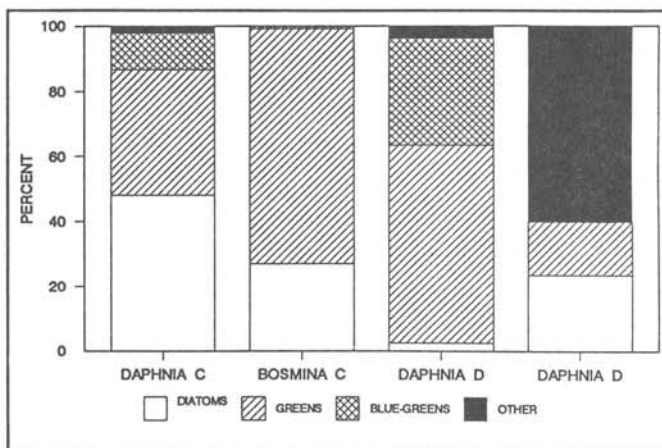


Figure 11  
Percent composition of gut contents of *D. parvula* and *B. longirostris* during Periods C and D.

## SEM SAMPLES

SEM micrographs of gut contents from zooplankton collected outside the four periods show that copepods can feed heavily on *M. granulata*. For example, fecal pellets of *S. doerrii* taken from the Sacramento River at Decker Island (station 64) on July 29, 1985, were full of *M. granulata* fragments (Figure 12). In samples taken from the Sacramento River at Collinsville (station 60) on August 9, 1985, *M. granulata* appeared to be the major component of the diet of *E. affinis* and was present in *S. doerrii* (Figures 13 and 14). These were non-bloom periods for *M. granulata*.

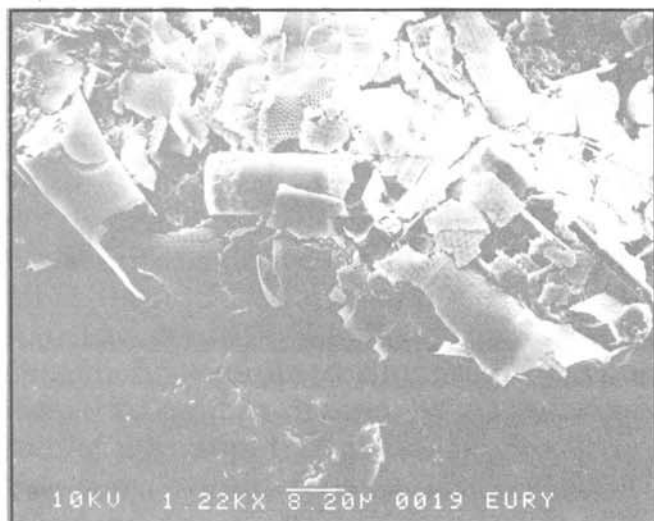


Figure 12  
Shattered *Melosira granulata* cells from a fecal pellet of *Eurytemora affinis* taken in the Sacramento River at Decker Island, 7/29/85.

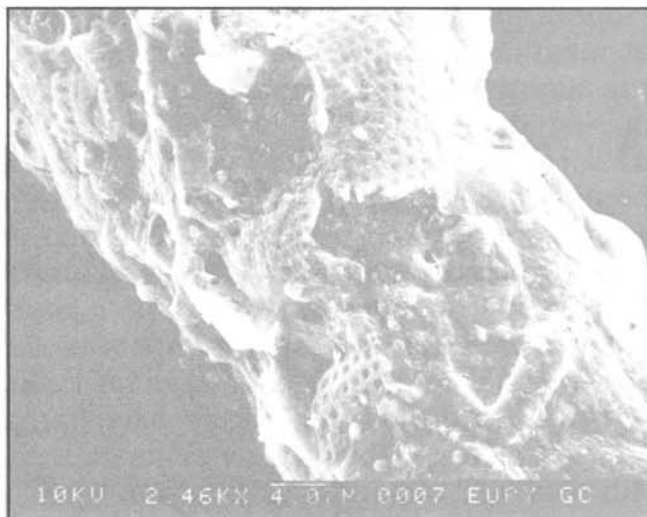


Figure 13  
*Eurytemora affinis* gut contents showing masses of *Melosira granulata* taken in Sacramento River at Collinsville, 8/9/85.

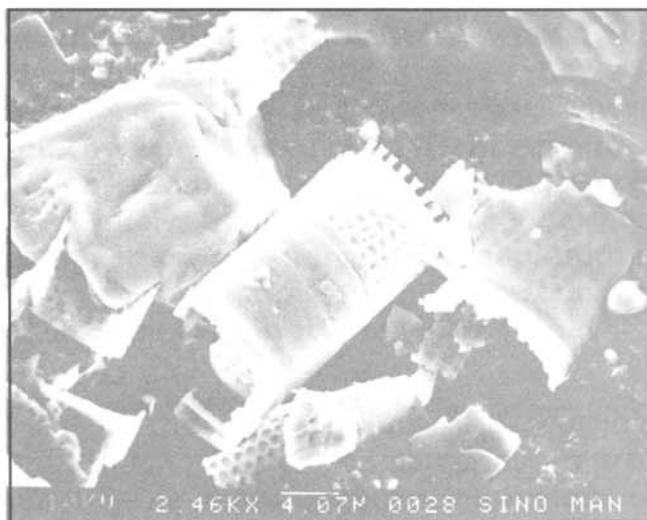


Figure 14  
*Melosira granulata* remains in the gut contents of *Sinocalanus doerrii* taken in the Sacramento River at Collinsville, 8/9/85.

## DISCUSSION

*Eurytemora affinis* and *S. doerrii* had similar food habits. *Thalassiosira* was the most abundant alga in both species and *S. potamos* was the second most abundant. Neither copepod showed any indication of having predatory habits. However, *S. tenellus*, a related Japanese species, has been shown to feed on its own nauplii in the laboratory (Hada and Uye 1991). Unless *S. doerrii* has a different feeding apparatus, which is unlikely, it should also prey on nauplii, not only its own but those of other species. Assuming that *S. doerrii* has the same ingestion rates as its congener, *S. tenellus*, chances of finding naupliar remains in its gut contents can be estimated. At naupliar concentrations of 400/liter, which would be close to the concentrations occurring during this study, the ingestion rates of adult *S. doerrii* would be about 20 nauplii/copepod/day (Hada and Uye 1991). Since gut residence time is about 1 hour for calanoids (Dagg and Grill 1980; Bautista *et al* 1988) most of the *S. doerrii* specimens examined should have contained naupliar remains. At an ingestion rate of 20 nauplii/copepod/day, however, *S. doerrii* would have a large negative effect on the *E. affinis* population size, even though the overlap in distribution of the two species is incomplete. Since no large decrease in *E. affinis* occurred after *S. doerrii* was introduced, it seems unlikely that *S. doerrii* preys extensively on *E. affinis*. Only laboratory experiments can answer the predation question definitively.

Both copepods consumed a wide variety of sizes, shapes, and species of diatoms and other algae. This agrees with literature results of gut examinations of field-caught copepods (Turner 1984, 1985). Although copepods are capable of selec-

tive feeding, they are essentially opportunistic feeders that will eat whatever is in the water if desirable food items are not available (Turner 1984). *Skeletonema potamos* forms short chains that can make it especially vulnerable to copepod grazing. Unlike solitary diatoms such as *Thalassiosira* that are captured one at a time, a chain of *S. potamos* will be caught all at once, yielding a high catch per effort for this species. Yet because of the small size of *S. potamos* cells, a single *Thalassiosira* may have a greater volume than a chain of *S. potamos*. The size difference between these diatoms is illustrated in Figure 2.

The cladocerans consumed more green algae than the copepods did. Green algae is generally more abundant in the San Joaquin River at Stockton, where the cladocerans were found, than in the Sacramento River and Suisun Bay, where the copepods were found (Department of Water Resources 1986, 1987). Therefore, it is likely that the difference in food composition between these zooplankton groups simply reflects the difference in algal composition in the water.

Most of the gut contents of *D. parvula* and *B. longirostris* consisted of an unidentifiable mass of particles, much of which was probably mineral matter and some of which could have been detritus. This is typical of results from other areas. In Polish lakes, cladocerans contained few algal cells; most of their gut contents were unidentifiable (Gliwicz 1969). In Lake Balaton, Hungary, the primary component of cladoceran gut contents was abioseston, mineral particles with organic matter adsorbed onto the surface (G.-Toth 1984).

Although some investigators have done quantitative studies of gut contents (Infante 1978, G.-Toth *et al* 1987), the accuracy of such studies is affected by the degree of digestion of the food and differential digestion of diatoms and soft-bodied algae. In this study, the SEM micrographs show that the *S. potamos* and *Thalassiosira* cells are reasonably intact but the *M. granulata* frustules are sometimes so shattered that determining the number present is not possible. In the phase-contrast work, however, only a few *M. granulata* cells were seen, and these were largely intact. Cell fragments were present but were not numerous, so accurate counts of cells could be made. On the other hand, the pennate diatoms found in the cladocerans during Periods C and D (Tables 4 and 5) were so fragmented that their volumes could not be calculated. Diatoms are, thus, likely to be more important to the cladocerans than indicated in these tables.

The degree of digestion as well as the cell volume must be considered in assessing the relative importance of different phytoplankton groups. Infante (1978) found various percentages of digested cells to total cells in copepods and cladocerans, ranging from zero for most blue-green algae to 33-100% for green algae to 100% for diatoms. She defined digestion as the absence or modification of cell contents. In the present study, all diatoms appeared to suffer damage to the frustules that would result in the loss of cell contents. Some of the green algae, especially *Scenedesmus* and flagellates, had either missing cell contents or damaged cell walls. All of the blue-green algae appeared to be intact.

The blue-green alga *Anacystis* was initially difficult to identify. It is a very small, 5- $\mu$ m-diameter alga, with few distinguishing features. Globules of unknown

origin can mimic it. Only after many slides had been examined could it be identified with confidence. Another blue-green species, *Agmenellum*, is even smaller, but when present in colonies it is unmistakable and its appearance in colonies enabled isolated cells to be recognized.

*Melosira granulata* was consumed by all the species studied, but it was not abundant in any of the zooplankton examined with the phase-contrast microscope, even during its bloom. Copepods had empty guts at the bloom stations, yet the SEM work shows that they consumed considerable quantities of *M. granulata* when concentrations were lower. The long chains present during blooms may inhibit handling. In a laboratory study, the copepod *Diaptomus* ate significantly more *Melosira* of 260  $\mu$ m mean chain length than several other types of algae (Fulton 1988). When *M. granulata* chains are short, copepods may select for it in the same way that *E. affinis* apparently does for *S. potamos*. That is, encounters with short chains enables the intake of a large number of cells in a short period of time.

The cladocerans continued to feed during the *M. granulata* bloom, but evidence from other studies suggests they may have been adversely affected. During blooms of filamentous blue-green algae, *Daphnia* decreases its filtering rate, increases the rejection rate of material that enters its valves, and has smaller brood sizes (Porter and McDonough 1983). *Bosmina*, which is smaller than *Daphnia*, does not increase its rejection rate because fewer filaments enter its valves, and its fecundity is not lowered (Porter *et al* 1982; Porter and McDonough 1983). *Daphnia* may react to *M. granulata* as it does to filamentous blue-green algae. *Daphnia* is a non-selective feeder that

has high feeding rates and takes whatever is in the water, including large colonial algae and inorganic particles. It cannot use taste to discriminate between low and high quality food items, as *Bosmina* can. *Bosmina* has lower feeding rates because of its taste discrimination and a different feeding apparatus (Burns 1968; Sarnelle 1986). The feeding capabilities of the two cladocerans are perhaps reflected in the heavy consumption of blue-green algae by *Daphnia* (Tables 4 and 5). These algae are considered to be poor quality food items (De Bernardi *et al* 1981; Holm *et al* 1983).

At high food concentrations, *Daphnia* outcompetes *Bosmina* (DeMott and Kerfoot 1982), but at low food concentrations such as have occurred in the Delta in recent years, the situation is reversed.

This may explain why *Daphnia* has experienced a long-term downtrend in abundance but *Bosmina* has not (Obrebski *et al* 1992).

In conclusion, *E. affinis* and *S. potamos* fed heavily on diatoms, particularly *Thalassiosira* and *S. potamos*. In the region of their greatest overlap, there is a potential for competition. Cladocerans consumed more green and blue-green algae than diatoms. This may be due to their location in the estuary rather than to actual differences in feeding habits. *Daphnia* and *Bosmina* have different feeding mechanisms, and these may explain why only *Daphnia*'s abundance has been reduced in recent years when phytoplankton concentrations have been low (Obrebski *et al* 1992).



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